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RESEARCH ARTICLE

The prey species and kleptoparasites of *Trichodes crabroniformis* (Coleoptera, Cleridae) – an active predator on flower-visiting insects in Bulgaria

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Abstract

Feeding of *Trichodes crabroniformis* (Fabricius, 1787) on insects from 10 families, belonging to orders Coleoptera, Hymenoptera and Hemiptera is documented under field conditions in Bulgaria. Cases of attacks on longhorn beetles of the species *Echinocerus floralis* (Pallas, 1773) clearly predominated, followed by those of the oedemerid beetles species *Oedemera femorata* (Scopoli, 1763). First concrete data on feeding of a member of the genus *Trichodes* Herbst on cantharidin-containing species of Oedemeridae are reported. The kleptoparasitic flies *Desmometopa sordida* (Fallén, 1820), *D. microps* Lamb, 1914 and *Neophyllomyza acyglossa* (Villeneuve, 1920) (Diptera, Milichiidae) are found to be attracted to individuals of *E. floralis* caught by the predator. The association of Milichiidae species with predatory Coleoptera, as well as with their coleopteran prey items is reported for the first time. This, previously unknown, food source for Milichiidae and the nature of the warning coloration in *T. crabroniformis* are also discussed.

Keywords

Cleridae, Milichiidae, behaviour, biology, insect prey, kleptoparasitism, mimicry.

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PENSOFT

Introduction

Trichodes crabroniformis (Fabricius, 1787) (Coleoptera, Cleridae) is one of the largest species of the genus *Trichodes* Herbst, known from Armenia, Bulgaria, Croatia, Greece, Italy (Sicily), North Macedonia, Slovenia and Asian Türkiye (Zimmermann 1971; Kolibáč 2006; Löbl et al. 2007; Löbl and Smetana 2013). In Bulgaria, this species has been reported from different regions, being most common in the southern part of the country (Kantardjiewa 1930; Ganev 1984). The biology of *T. crabroniformis* has not been specifically studied. Only Angelov (1964) mentioned that adults visit flowers of umbelliferous plants.

Larvae of *Trichodes* species develop in the larval cells of bees and wasps or feed on locust egg pods, while the adults are flower-visitors (Opitz 2002; Kolibáč 2010). Adults are best known as pollen feeders (Mawdsley 2002; Opitz 2002; Flügel 2014), but in fact, they often attack other flower-visiting insects, and thus, have a mixed diet (Assmuss 1865; Richter 1961; Foster 1976; Kolibáč 2010). Predation is often seen as an additional mode of feeding for these beetles (Linsley and MacSwain 1943; Kolibáč 2010; Flügel 2014). Biological and ecological studies of *Trichodes* species are more focused on the plants, on which these beetles feed, rather than to their insect prey (Foster 1976; Mawdsley 2002; Flügel 2014; Kurzeluk 2014). A number of earlier authors considered *Trichodes* adults as predators, and plant material as an additional food source (Assmuss 1865; Escherich 1892; Cros 1908). It is therefore not surprising that a substantial amount of the information about *Trichodes* prey items can be found in earlier studies (Assmuss 1865; Gaulle 1874; Cros 1908; Linsley and MacSwain 1943; Richter 1961; Foster 1976). But even in these reports, prey items were usually identified only to the order or family level. Therefore, we can assume that this aspect of the biology of the adults of *Trichodes* is generally neglected and understudied. Recently, after the isolation of the terpenoid toxin cantharidin from *T. apiarius* (Linnaeus, 1758) specimens (Fietz et al. 2002; Lückmann and Niehuis 2009), the diet of *Trichodes* species attracted the attention of scientists again. Cantharidin has a defensive role in insects, serving as a potent insecticide, antifeedant and vesicant (Fietz et al. 2002). The only known insects able to produce cantharidin belong to the beetle families Meloidae and Oedemeridae (Fietz et al. 2002). According to several authors (Fietz et al. 2002; Lückmann and Niehuis 2009; Bocakova et al. 2016) adults of the genus *Trichodes* may receive this toxin from the hemolymph of meloids or oedemerids.

In June 2022, the authors frequently observed adults of *T. crabroniformis* on inflorescences of plants belonging to the families Apiaceae and Asteraceae (e.g. *Onopordum acanthium*) in the vicinity of Ustrem Village (SE Bulgaria). In many of these cases, the beetles were found to feed on flower-visiting insects, which observations prompted the present study.

Materials and Methods

Material collection and field observations were carried out by the authors in the the vicinity of Ustrem Village (Sakar Mts) during four consecutive days – from June 30 to July 3, 2022. Adults of *T. crabroniformis*, their prey and associated kleptoparasites were collected from inflorescences of *Torilis arvensis* subsp. *neglecta* (coordinates 42°01.374'N; 26°26.975'E) and *Chaerophyllum byzantinum* (coordinates 42°01.357'N; 26°26.900'E) (Apiaceae) in two nearby localities (Fig. 1 A, B). Both localities are in the boundaries of alfalfa (*Medicago sativa*) fields, adjacent to riparian vegetation. The tree vegetation in the vicinity is mainly represented by willows (*Salix* spp.), black poplar (*Populus nigra*) and black alder (*Alnus glutinosa*). The studied habitats are located at an altitude of approx. 100 m above sea level. During the study period, the weather was dry and sunny, with maximum air temperature of 28 – 30°C.

Most of the *T. crabroniformis* specimens captured together with their prey material and the kleptoparasitic flies, were hand-collected in individual plastic tubes filled with 70% ethanol (individual samples). Additionally, several specimens of *T. crabroniformis* as well as their prey items from the cerambycid species *Echinocerus floralis* (Pallas, 1773), were collected together in a single container with 70% ethanol as a composite sample.

Specimens of Oedemeridae were identified by Ognyan Sivilov (Sofia University "St. Kliment Ohridski"), and those of Hymenoptera by Toshko Ljubomirov (Institute

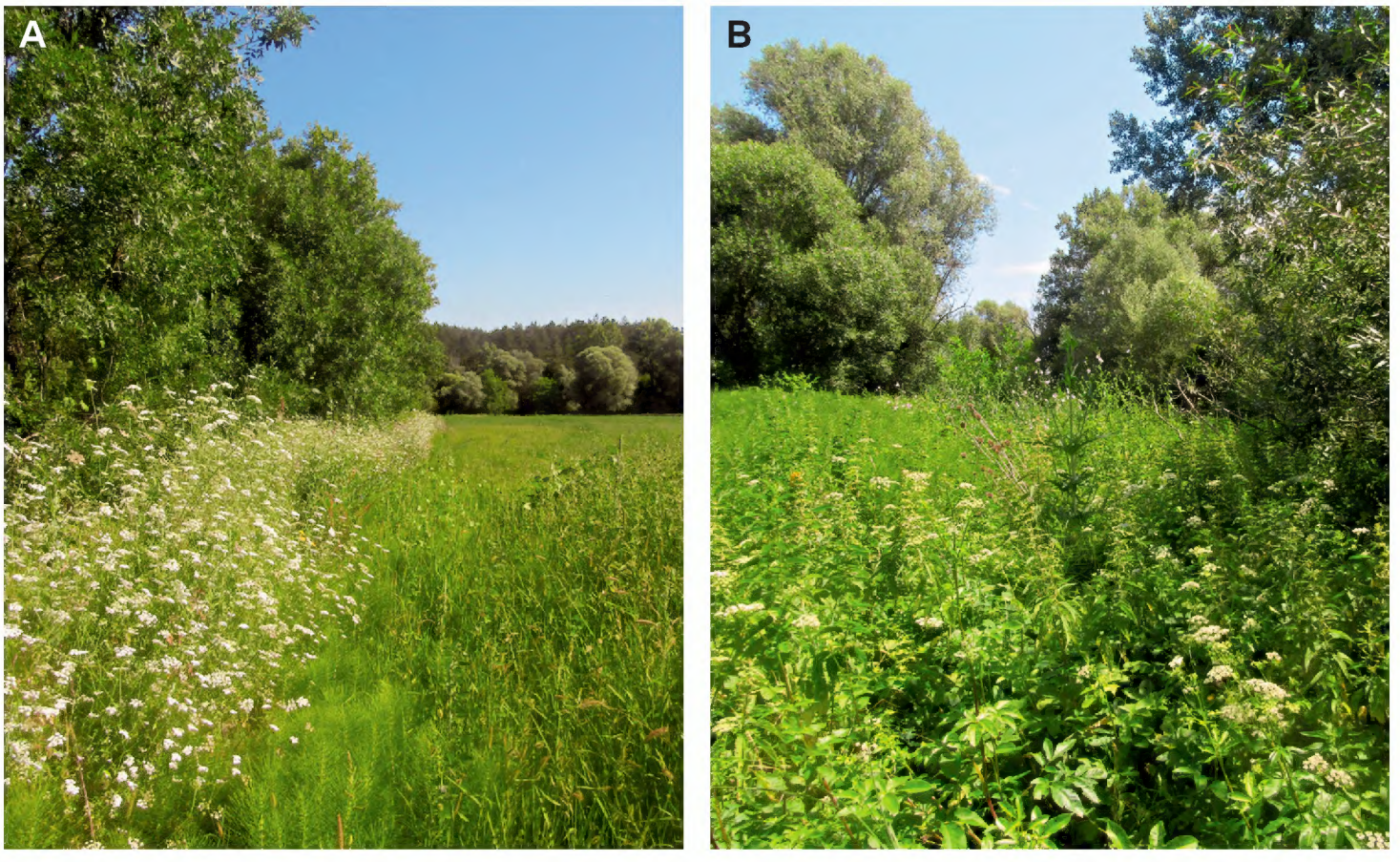

Figure 1. Feeding habitats of *Trichodes crabroniformis* in the vicinity of Ustrem Village (Sakar Mts): **A** Boundary of an alfalfa field with *Torilis arvensis* subsp. *neglecta*; **B** Riverine meadows with *Chaerophyllum byzantinum*.

of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences). Insects from the remaining taxa, including the specimens of *T. crabroniformis* and kleptoparasitic flies (Diptera, Milichiidae), were identified by the first author. For the identification of Milichiidae specimens, several taxonomic papers were used (e.g. Papp 1978, 1993; Sabrosky 1983; Iwasa 1996). The identified taxa of *Desmometopa* Loew were compared with those from the Diptera collection of V. Beshovski (Entomological and Arachnological Collections of Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences (IBER)).

The pictures were taken with a digital camera Canon PowerShot SX420 IS (Figs 1, 3) and a combination of Canon EOS 2000D digital camera, PRO-CA Camera Adapter and microscope Olympus SZ61 (Figs 2, 4, 5). The collected specimens are preserved in the Zoological Collection of Sofia University, Faculty of Biology (BFUS).

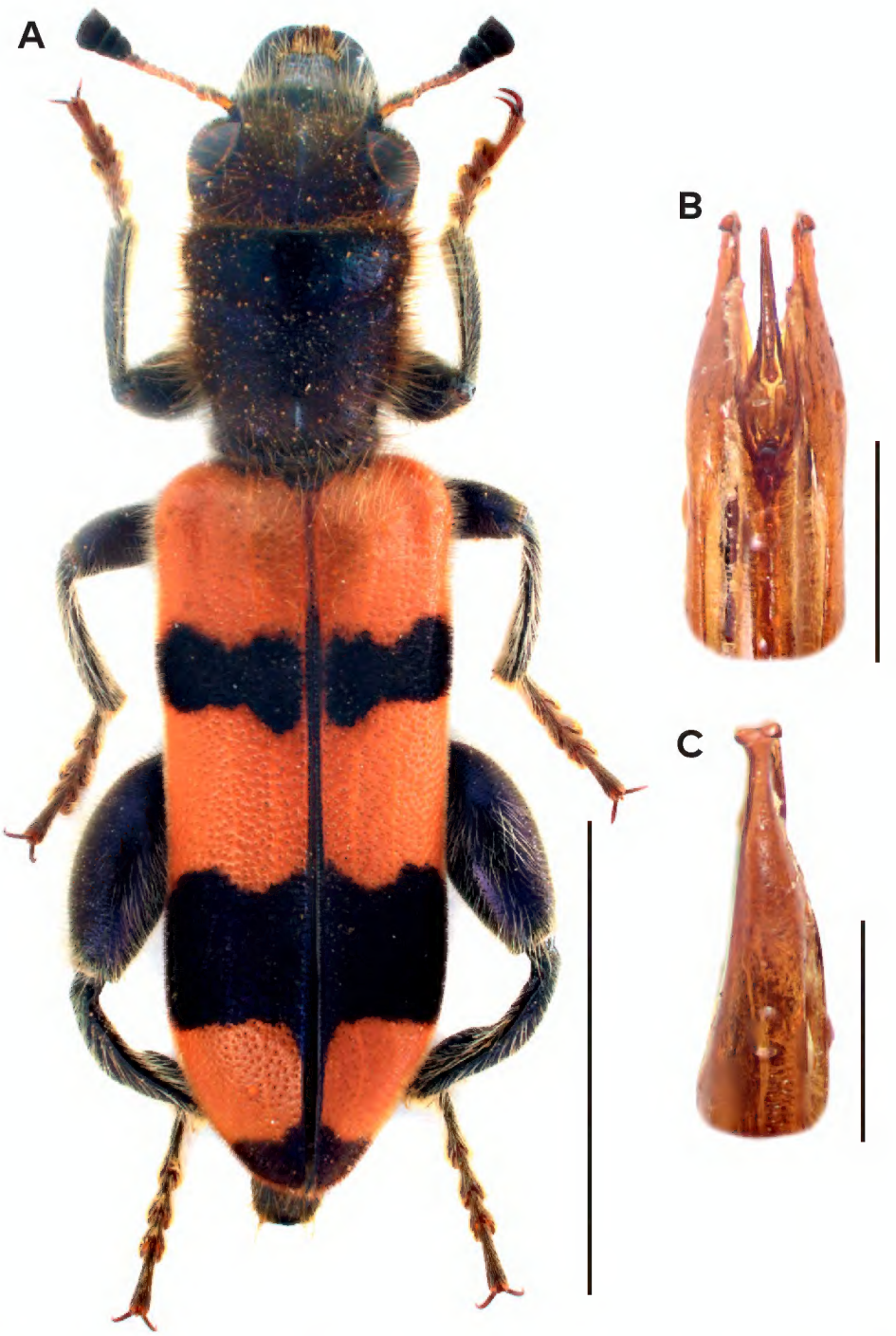

Figure 2. Male of *Trichodes crabroniformis* from Ustrem Village (Sakar Mts): **A** Habitus; **B** Apex of aedeagus, ventral view; **C** Apex of aedeagus, lateral view. Scale bars: **A** = 10 mm; **B**, **C** = 1 mm.

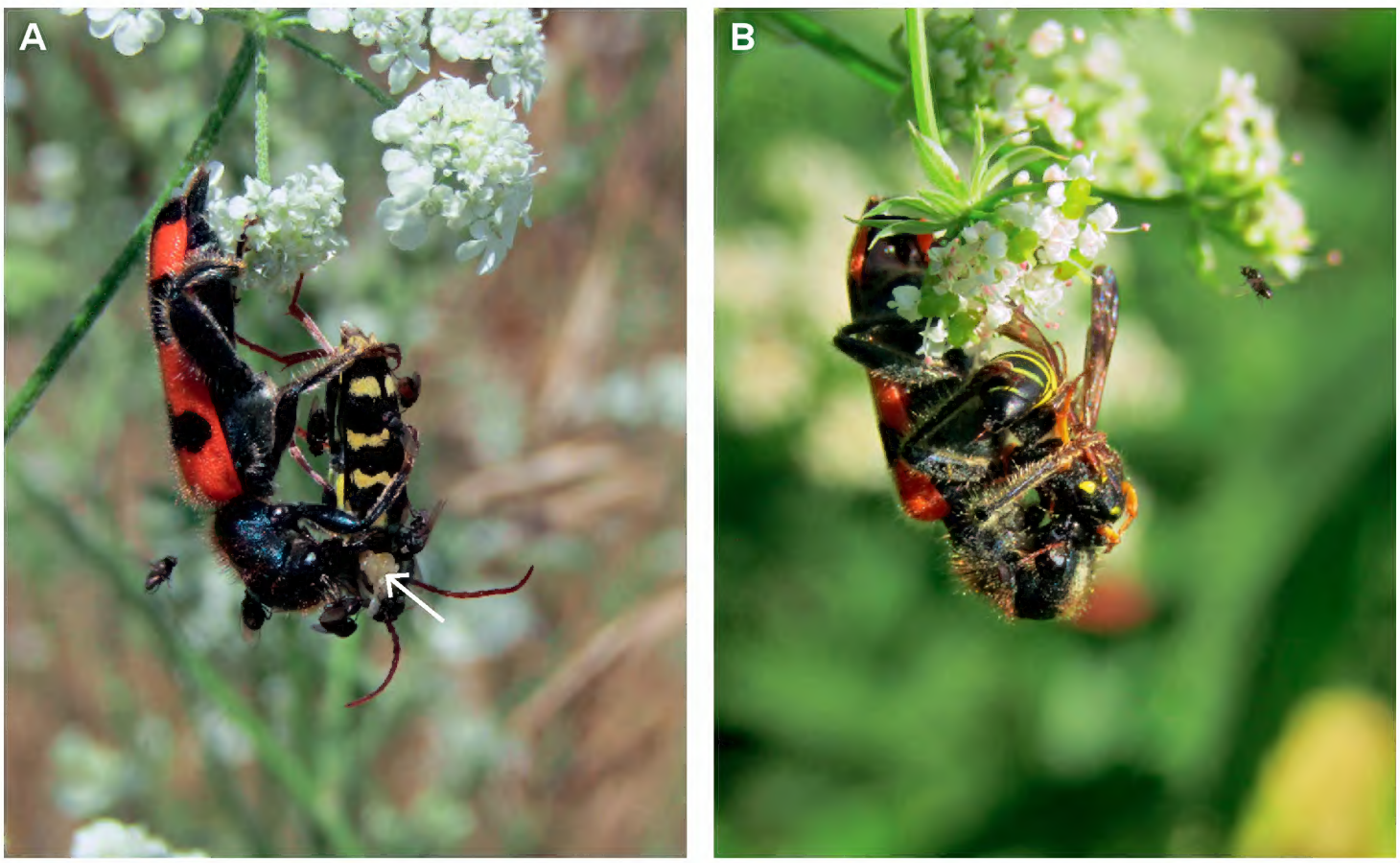

Figure 3. *Trichodes crabroniformis* attacking prey: **A** Attack on *Echinocerus floralis* (Cerambycidae) on inflorescence of *Torilis arvensis* subsp. *neglecta* (arrow indicate the nematode juvenile emerging from the host); **B** Attack on *Hemipterochilus bembeciformis terricola* (Vespidae: Eumeninae) on inflorescence of *Chaerophyllum byzantinum*.

Results

A total of 24 individual samples were collected, supplemented by one composite sample with five *Trichodes* specimens, together with their prey item. Thus, a total of 29 cases of predation of *T. crabroniformis* on flower-visiting insects were documented during the study period. Ten insect families of three orders were recorded as prey of *T. crabroniformis*: Miridae (Hemiptera); Cantharidae, Coccinellidae, Mycteridae, Oedemeridae and Cerambycidae (Coleoptera); and Bembicidae, Vespidae, Formicidae and Andrenidae (Hymenoptera) (Table 1). Eleven species of these families were identified, and two more taxa of Hymenoptera (*Formica* sp. and *Andrena* sp.) were identified to the genus level. Insects of the order Coleoptera were most the often attacked group (24 cases, or nearly 83% of those recorded). Cases of attacks on individuals of the longhorn beetle species *E. floralis* clearly predominated our recordings (14 recorded cases) followed by those of *Oedemera femorata* (Scopoli, 1763) (four cases). Attacks on insects of the remaining species were recorded only once in the present study.

Prey insects were damaged in varying degree at the moment of observation, depending on the stage of the feeding process (Figs 3, 4). After capturing its prey, adults of *T. crabroniformis* use their mandibles to kill the insects usually by rupturing membranes between the head and the prothorax as well as between the prothorax and

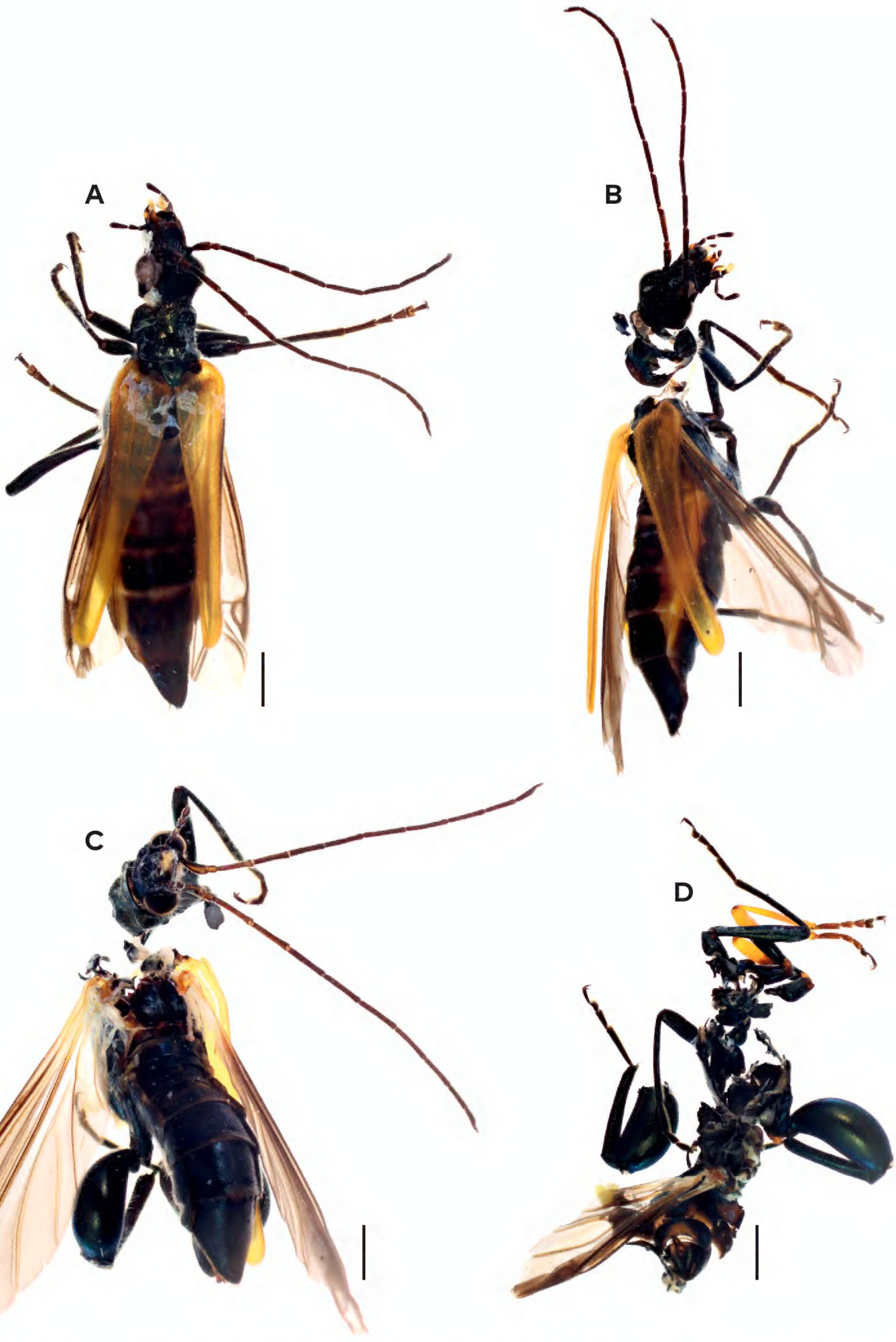

Figure 4. Specimens of Oedemeridae, captured by *Trichodes crabroniformis*: **A–C** *Oedemera femorata*; **D** *O. flavipes*. Scale bars = 1 mm.

the mesothorax, often without the full fragmentation of the body parts (particularly in the cases of *E. floralis* and *Oedemera* spp.). In some cases the head or the prothorax of the prey were also crushed in the attack. Then the predator ingested the soft tissues, starting from the prothorax and progressing to the posterior end of the body. In three of the four observed cases of attack on Hymenoptera, the head of the prey was removed prior to feeding.

Adults of *T. crabroniformis* were observed to feed on pollen throughout the day, but in the warm hours, when the activity of other flower visiting insects increases, the main mode of feeding was predation. Thus, at 9 to 10 a.m. on July 3rd, a total of 24 adult beetles were observed on flowers of *T. arvensis* subsp. *neglecta*. Some of these individuals were feeding on pollen, others were in resting position on, under or inside the inflorescences. On the same date, the first case of a captured insect was observed at 10 a.m. In the next 70 minutes, a total of 22 such cases were recorded, while only a few beetles were observed feeding on pollen at the same period.

Figure 5. Kleptoparasitic flies (Diptera: Milichiidae) of *Trichodes crabroniformis*: **A** *Neophyllomyza acyglossa*, female; **B** *Desmometopa sordida*, male; **C**, **D** *D. microps*, males. Scale bars = 1 mm.

Table 1. Prey insect species of *Trichodes crabroniformis* in the vicinity of Ustrem Village: Mp – number of males; Fp – number of females; N – total number of prey specimens; STr – sex of *Trichodes* specimens; M – male/s; F – female/s; TA – *Torilis arvensis* subsp. *neglecta*; CB – *Chaerophyllum byzantinum*.

Prey species	Mp	Fp	N	STr	Plants
Order Hemiptera					
Family Miridae					
1. *Deraeocoris ruber* (Linnaeus, 1758)	1		1	F	TA
Order Hymenoptera					
Family Bembicidae					
2. *Gorytes quinquecinctus* (Fabricius, 1793)		1	1	F	CB
Family Vespidae					
3. *Hemipterochilus bembeciformis terricola* (Mocsáry, 1883)		1	1	F	CB
Family Formicidae					
4. *Formica* sp.	1		1	F	TA
Family Andrenidae					
5. *Andrena* sp.		1	1	F	TA
Order Coleoptera					
Family Cantharidae					
6. *Rhagonycha fulva* (Scopoli, 1763)		1	1	F	TA
Family Coccinellidae					
7. *Coccinella septempunctata* Linnaeus, 1758	1		1	F	TA
Family Mycteridae					
8. *Mycterus curculionoides* (Fabricius, 1781)		1	1	F	TA
Family Oedemeridae					
9. *Oedemera femorata* (Scopoli, 1763)	2	2	4	M, F	TA
10. *Oedemera flavipes* (Fabricius, 1792)	1		1	F	TA
Family Cerambycidae					
11. *Stenurella bifasciata* (O.F. Müller, 1776)	1		1	F	TA
12. *Stictoleptura fulva* (De Geer, 1775)		1	1	M	TA
13. *Echinocerus floralis* (Pallas, 1773)	1	13	14	M, F	TA, CB

During the entire observation period, feeding of *T. crabroniformis* on insects was observed from 10 a.m. to 7 p.m. Both male and female of the species exhibited predatory behaviour. Like Foster (1976), and contrary to the record of Linsley & MacSwain (1943), we have not observed cannibalism in *Trichodes*. In the evening after 7 p.m., *T. crabroniformis* specimens were observed resting on or under inflorescences, apparently remaining in this position until the next morning.

Kleptoparasitic flies of the family Milichiidae were observed in a number of cases after the attack of *T. crabroniformis* on *E. floralis* and in one case of attack of

T. crabroniformis on *Hemipterochilus bembeciformis terricola* (Mocsáry, 1883) (Fig. 3A, B). Flies were observed licking hemolymph on the freshly captured prey or were perched on the predator as well as on the inflorescences around. The predator apparently ignored the presence of the flies. A total of 73 fly specimens were collected from *E. floralis* (Table 2), of which 35 were found in the individual samples and 38 in the composite sample. Three Milichiidae fly species were identified: *Desmometopa sordida* (Fallén, 1820) (31 males and 18 females), *D. microps* Lamb, 1914 (eight males and six females) and *Neophyllomyza acyglossa* (Villeneuve, 1920) (10 females) (Fig. 5).

In one case of attack of *T. crabroniformis* on *E. floralis*, the emergence of a nematode juvenile of the family Mermithidae from the remainings of the body of the prey specimen was observed (Fig. 3A). After dissection of the same beetle individual in the laboratory, a second mermithid specimen was found coiled in the abdominal region of the host. The poor condition of the fixed material and the juvenile stage of the nematodes, however, did not allow amore precise identification.

Discussion

The available data on the prey preferences of adults of the genus *Trichodes* are scarce and incomplete. According to Assmuss (1865), adults of the genus are found mainly on Umbelliferae (= Apiaceae) and Spiraeaceae (= Rosaceae), where they feed on pollen, but mainly prey on insects that visit these flowers. Gaulle (1874) reported feeding of *T. alvearius* (Fabricius, 1792) with an unidentified Hymenoptera species. Cros (1908) describes two cases of attack of *T. umbellatarum* (A. G. Olivier, 1795) on *Heliotaurus erythrogaster* (Lucas, 1846) (sub *Omophlus erythrogaster* Luc.) and a bee. According to Linsley and MacSwain (1943), the prey preferences of *T. ornatus* Say, 1823 are represented by „mostly small Coleoptera". Richter (1961) reports feeding of adults of *T. longissimus* (Abeille de Perrin, 1881), *T. apiarius* and *T. insignis* Fischer von Waldheim, 1829 with beetles from the families Oedemeridae, Melyridae and Coccinellidae, but does not specify the prey species. Foster (1976) summarizes that *Trichodes* beetles feed on a „wide range of soft-bodied insects that are attracted to flowers".

Table 2. Kleptoparasitic flies of the family Milichiidae, associated with *Trichodes crabroniformis* and its prey species *Echinocerus floralis* in the vicinity of Ustrem Village: Mf – number of males; Ff – number of females; N – total number of fly specimens; STr – sex of *Trichodes* specimens; M – male/s; F – female/s; TA – *Torilis arvensis* subsp. *neglecta*; CB – *Chaerophyllum byzantinum*.

Fly species	Mf	Ff	N	STr	Plants
Desmometopa sordida (Fallén, 1820)	31	18	49	M, F	TA, CB
D. microps Lamb, 1914	8	6	14	M, F	TA, CB
Neophyllomyza acyglossa (Villeneuve, 1920)		10	10	M, F	TA, CB

The species of Oedemeridae of the European fauna with verified presence of cantharidin are *Nacerdes melanura* (Linnaeus, 1758), *Oedemera femorata* (Scopoli, 1763), *O. flavipes* (Fabricius, 1792), *O. lurida* (Marsham, 1802), *Chrysanthia geniculata* W. L. E. Schmidt, 1846 and *Ch. viridissima* (Linnaeus, 1758) (Vázquez 2002). Two of these species – *O. femorata* and *O. flavipes*, were among the prey of *T. crabroniformis* in the present study, confirming feeding of beetles of the genus *Trichodes* on cantharidin-containing species of Oedemeridae.

Our observations show that highly sclerotized (e.g. *E. floralis*, *Stictoleptura fulva* (De Geer, 1775), *Mycterus curculionoides* (Fabricius, 1781) and *Coccinella septempunctata* Linnaeus, 1758) and relatively large insects can serve as a prey for *T. crabroniformis*. It is noteworthy that most of the attacked insects in our study possess defensive or venom glands (*Deraeocoris ruber* (Linnaeus, 1758) and aculeate Hymenoptera), contain toxic compounds in their hemolymph and body tissues (*C. septempunctata* and the species of Oedemeridae), or are mimics of defended species (*E. floralis*) (Table 1). These insect species, however, were also among the most abundant flower-visitors in the studied habitats during the observation period. For example, alfalfa (*M. sativa*) is among the main host plants of *E. floralis* (Sama 2002), and this longhorn beetle species is common in alfalfa fields of Bulgaria (Toshova et al. 2010; Imrei et al. 2014). Therefore, the prevalence of *E. floralis* in the diet of *T. crabroniformis* may be due to its abundance in the studied habitats, all located nearby to alfalfa fields. Studies in other habitat types with a different composition of potential prey species will help to clarify whether *T. crabroniformis* indeed prefers defended or mimetic species, or is rather a generalist predator on flower-visiting insects.

Like other species of the genus *Trichodes* (e.g. *T. apiarius*, *T. favarius* (Illiger, 1802), *T. punctatus* Fischer von Waldheim, 1829), *T. crabroniformis* exhibits a mixture of red or orange and metallic blue color patterns (blue-black in *T. crabroniformis*) (Opitz 2002; Zimmermann 1971) (Fig. 2). Such pattern is considered a warning coloration in clerids (Bocakova et al. 2016). In general, the warning coloration in *Trichodes* has been considered to display Batesian mimicry (Mawdsley 1994; Bocakova et al. 2016). In Batesian mimicry, an edible species copies the warning signal of a defended, while in Müllerian mimicry, different defended species share a common warning signal (Speed 1999). According to Batesian mimicry, some species of the genus *Trichodes* mimic aculeate Hymenoptera while others (including *T. crabroniformis*) mimic flower-visiting species of Meloidae (Coleoptera) or Zygaenidae (Lepidoptera) species (Mawdsley 1994). However, after the isolation of toxic compounds from *T. apiarius* (Fietz et al. 2002; Lückmann and Niehuis 2009), mimicry in the genus *Trichodes* could be considered a variant of Müllerian mimicry, since the beetles are chemically defended (Lückmann and Niehuis 2009). The feeding of *T. crabroniformis* with toxic prey species reported in the present study confirms the latter concept and raises the challenge of further investigations of the relationship of this predator with other aposematic species in the ecosystem.

Flies belonging to several genera of the family Milichiidae are known to be attracted to the insect prey of spiders from the families Araneidae, Thomisidae and

Salticidae or of some predatory insects, such as assassin bugs (Reduviidae), robber flies (Asilidae) and mantids (Mantodea) (Sabrosky 1983; Sivinski 1985; Petrischak and Ulrich 2012). These flies feed on the hemolymph of freshly killed insects and are considered kleptoparasites (Sivinski and Stowe 1980; Eisner et al. 1991; Sivinski et al. 1999). Insects belonging to the orders Hymenoptera and Hemiptera, when captured by predators, are known to be attractive to kleptoparasitic flies (Eisner et al. 1991). The present record is the first to demonstrate the association of Milichiidae species with predatory Coleoptera, as well as with attacked insects from the same order. It has been reported that kleptoparasitic flies are attracted to defensive volatile compounds, released by heteropterans, as well as to venom compounds of social vespids (Eisner et al. 1991; Zhang et al. 2021). It can be assumed that *E. floralis* may release some kind of volatile kairomones. On the other hand, visual stimulus could also play a role in attracting the kleptoparasites, given the warning coloration of *E. floralis*, which resembles that of a number of aculeate Hymenoptera. In this line of thought, *T. crabroniformis* possesses a warning coloration, and it is possible that flies are fooled by this predator-prey combination in which both participants visually resemble their usual food source.

Two fly species identified in the present study – *D. sordida* and *N. acyglossa* – have been previously recorded from Bulgaria (Hubenov 2021). The second species of *Desmometopa* – *D. microps* – is reported for the first time for the country. The adults of *D. microps* are known flower visitors (Iwasa 1996; Papp and Wheeler 1998; Roháček 2009) and a kleptoparasitic association is reported for the first time for this species. The adults of *D. sordida* are known to feed on prey insects (particularly honeybees) of spiders and assassin bugs (Sivinski and Stowe 1980; Sabrosky 1983; Sivinski 1985). Kleptoparasitism has not been reported for *N. acyglossa*, but it is known for other species of the genus *Neophyllomyza* Melander (Sivinski and Stowe 1980; Eisner et al. 1991; Sivinski et al. 1999). Feeding of *N. acyglossa* on dead insects is noted by Shtakelberg (1970) and Papp (1978).

Surprisingly, in the present research males of *D. sordida* and *D. microps* males predominated in number among the collected specimens of these species (Table 2). Our data contradict to most observations on kleptoparasitic flies, in which the collected flies have been almost exclusively females (Sivinski 1985; Sivinski et al. 1999; Zhang et al. 2021). We did not consider the flies sex or feeding and mating behaviour in the field observations, and therefore we could not propose a reasonable suggestion for the prevalence of the male specimens in the samples.

Our data suggest that *T. crabroniformis* is an active predator on a variety of flower-visiting insects, at least from the orders Coleoptera and Hymenoptera, and it is also involved in specific host-kleptoparasite interaction. The observed attack frequency suggests that the species may contribute substantially to the adult mortality in the populations of the attacked insects. It is possible that the larger body size, compared to the majority of species of genus *Trichodes*, favours the predation in this species. Further studies on the diet and other aspects of the biology of *Trichodes* will help

to elucidate the behavioural interactions of these clerids with other species in the ecosystem.

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